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Andromonoecy and carpenter-bee pollination in *Solanum melongena* var. *insanum, S. surattense* and *S. torvum* (Solanaceae)

Ch. Bhaskar Rao[1], **AJ Solomon Raju**[2*]

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Author Affiliation:
[1]Department of Botany, Government College for Women (A), Guntur - 522 001, Andhra Pradesh, India
[2]Department of Environmental Sciences, Andhra University, Visakhapatnam 530 003, Andhra Pradesh, India

[*]Corresponding author
Department of Environmental Sciences, Andhra University,
Visakhapatnam 530 003,
Andhra Pradesh, India
Email: solomonraju@gmail.com

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ABSTRACT

Solanum melongena var. *insanum, S. surattense* and *S. torvum* are andromonoecious and self-compatible and pollinated by carpenter bees. Andromonoecy is not perfectly evolved as female sterile flowers are produced in a small percentage at plant level. Carpenter bees are the appropriate pollinators since they display buzzing behavior to release pollen from poricidal anthers. The three *Solanum* species act as exclusive pollen source for carpenter bees and other bees that visit their flowers due to non-production of nectar by them.

Keywords: *Solanum melongena* var. *insanum, S. surattense*, *S. torvum*, andromonoecy, self-compatibility, carpenter bees.

1. INTRODUCTION

The family Solanaceae has about 100 genera consisting of 2,500 species distributed world over with species diversity centered in America, Australia and Africa (Olmstead et al., 1999; 2008). In India, this family is represented by 29 genera with 116 species, 2 sub-species, 3 varieties and 1 forma (Reema Kumari, 2004). Of these, 12 genera with 39 species are distributed in the Eastern Ghats region (Venkatappa, 2011). In this family, *Solanum* with about 1500 species is one of the largest genera distributed throughout the world (Vorontsova et al., 2013). In India, this genus is represented by 49 species which are distributed throughout the country, of which 17 species occur in the Eastern Ghats region (Venkatappa, 2011). In this genus, *S, lycopersicum* (tomato), *S, melongena* (eggplant) and *S. tuberosum* (potato) are major crops of global agriculture.

Andromonoecy is more common in Solanaceae family and it is well documented in *Solanum* genus (Vorontsova et al., 2013). In *Solanum* genus, a number of species display andromonoecy and dioecy as functional sexual systems. In vast majority of dioecious species, the female flowers produce pollen-bearing anthers but the pollen is inaperturate, viable and does not

produce a pollen tube while male flowers produce pistils with ovules (Martine and Anderson, 2006). In and romonoecious species, the staminate flowers produce variously or noticeably reduced pistil because the style is short to place the stigma above the staminal column. As a result, the stigma is unable to receive pollen directly from the pollinating bees but there is a possibility for incidental gravitational pollination from pollen puffed into the air in the space between anthers by the sonicating action of probing bees (Vorontsova et al., 2013). Bawa and Beach (1981) reported that andromonoecism is functional in species pollinated by bats, bees, flies, hummingbirds and moths. Heithaus et al., (1974) stated that andromonoecy is evolved to selective pressure for increasing cross-fertilization. Zapata and Arroyo (1978) mentioned that andromonoecism is a result of abortion of non-functional pistils in certain flowers that serve as male or attraction functions before their anthesis. These authors suggested three possibilities as to the significance of pistils in bisexual flowers that largely serve as pollen donors. First, the abortion of pistils could structurally perturb the floral morphology which in turn could disrupt the pollination mechanism. Second, the abortion of pistils in many bisexual flowers prior to pollination could restrict the efficacy of selection on progeny acting through control over pollen germination and tube growth, and embryo and fruit abortion. Third, the abortion of pistils may not occur in most hermaphroditic species because it is not possible to predict the fate of flowers as pollen donors or pollen recipients before pollination (Lloyd, 1980).

Despite the *Solanum* genus being speciose in India, many species have not been investigated in detail for their floral ecology, sexual systems and pollination aspects. In this context, the work reported in this paper was done to describe these aspects for *S. melongena* var. *insanum* L, *S. surattense* Burm and *S. torvum* Sw. to the extent possible for documentation to serve as reference information for future workers in this direction.

2. MATERIALS AND METHODS

Solanum melongena var. *insanum* growing in the croplands of the outskirts of Ongole in Prakasam District, *S. surattense* in wild pockets of Bhimili area and *S. torvum* in the wild pockets of Araku area in the State of Andhra Pradesh, India, were used for the present study during March 2021 to April 2022. These plant species were observed in the field for their flowering period, flower opening schedule and anther dehisce mode. The flowers were examined for their floral morphological and functional traits and these detailed are recorded. The pollen grains characteristics were also noted as feasible. Flowers visitors to all three plant species were carpenter bees and digger bees with the first category as most common. The daily foraging visits made on selected number of flowers of each plant species by each carpenter bee species were pooled and presented as daily percentage of foraging visits made by them in Figure 1. Since the flowers of all three plant species are functionally andromonoecious, the fruit set in hermaphrodite and female-sterile flowers were observed and the finding is noted. Bud and flower-feeding insects in these species were observed with reference to their negative role in the success of sexual reproduction.

OBSERVATIONS

Floral biology

S. melongena var. *insanum* is an armed sub-shrub (Figure 1a), *S. torvum* a small shrub (Figure 4a) and *S. surattense* a small perennial prostrate shrub (Figure 2a). The flowering occurs during April-November in *S. melongena* var. *insanum*, May-August in *S. surattense* and August-November in *S. torvum*. But, sparse flowering also occurs outside this period in all these three species depending on the soil nutrient and moisture status. The flowers are extra-axillary, mostly solitary in *S. melongena* var. *insanum* (Figure 1b), borne as 3-5 flowered clusters in leaf axils in *S. surattense* (Figure 2b) and many-flowered corymbose cyme borne supra-axillary in *S. torvum*. The flowers are oriented horizontally or slightly erect, odourless and actinomorphic in all three species. The calyx has 5 lanceolate stellate-pubescent lobes in *S. melongena* var. *insanum,* 5 green, prickly and inconspicuous sepals in *S. surattense* and 5 small green hairy sepals which are basally connate and free towards apex in *S. torvum*. The corolla has 5 bluish-violets with triangular lobes with acute apex in *S. melongena* var. *insanum*, 5 large purple conspicuous petals in *S. surattense* and 5 white basally connate and rotating petals in *S. torvum*. The stamens are 5 with filaments tipped with long vertically held yellow anthers in all three plant species (Figure 1d, Figure 4c). The ovary is many-ovuled in all three species (Figure 1h, Figure 3d, Figure 4g); the style is villous with a capitate-lobed stigma in *S. melongena* var. *insanum* (Figure 1f, g) and bi-lobed stigma in *S. surattense* and *S. torvum*. In all three species, the flowers are bisexual, distylous and represent long-styled (Figure 1c, Figure 2c-e, h-j, Figure 4b, e, f) and short-styled ones (Figure 2f, g, k, l) with the first type as most common. In both flower types, the pollen is produced and there is no difference in the size and structure of pollen grains but their viability levels were not examined. The pollen grains are dry, powdery, yellow and spheroidal to sub-prolate (Figure 1e, Figure 3b, c, Figure 4d). Fruit set was noted in long-styled flowers while there is no fruit initiation in short-styled flowers indicating the function of andromonoecy in these plant species. The fruit is a globose many-seeded

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greenish-dull white berry with enlarged fruiting calyx at the base in all three species (Figure 1i). The fruit color changes to light to bright yellow color when ripe.

In all three *Solanum* species, the flowers are open daily early in the morning during 0500-0830 h. The anthers dehisce poricidally through apical pores after anthesis (Figure 3a). Both long- and short-styled flowers are nectarless. In long-styled flowers, the placement of stigma above the anthers facilitates definite contact with the ventral side of the probing insect species which visits the flowers for pollen collection.

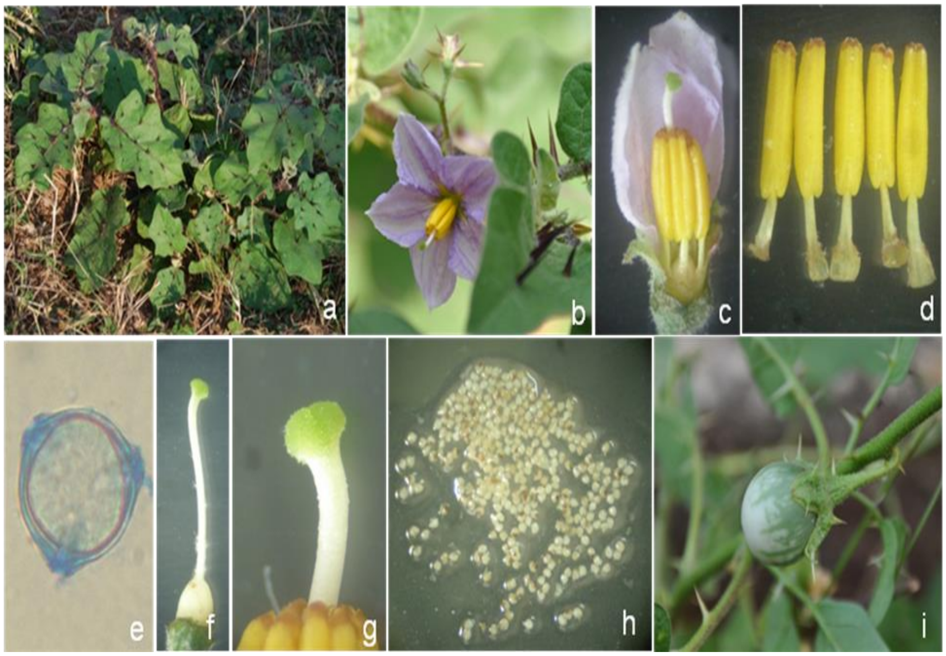

Figure 1 *Solanum melongena var. insanum*: a. Habit, b. Flower, c. Long-styled hermaphrodite flowers, d. Stamens, e. Pollen grain, f. Pistil, g. Style and Stigma, h. Ovules, i. Fruit.

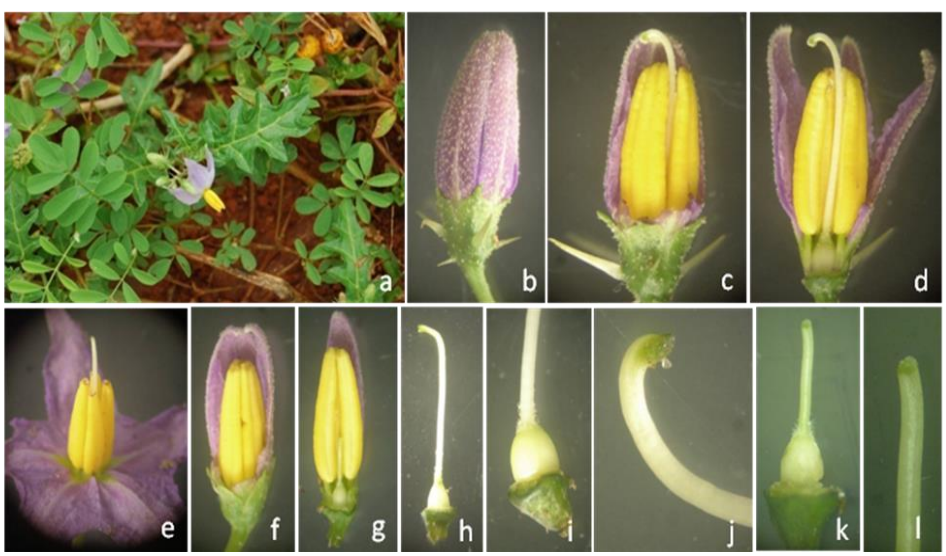

Figure 2 *Solanum surattense:* a. Habit, b. bud, c-e. Long-styled hermaphrodite flowers, f. & g. Short-styled flowers, h. Ovary with long style terminated with stigma, i. Ovary of long styled flower, j. Close-up view of stigma of long styled flower, k. & l. Ovary with short-style and stigma.

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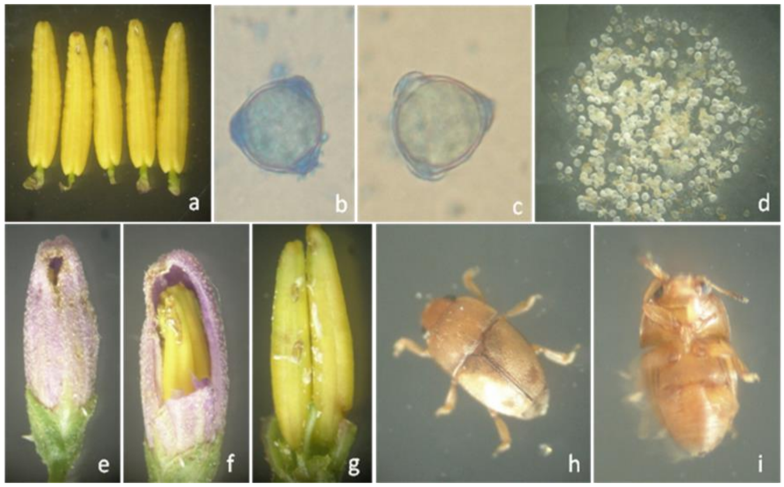

Figure 3 *Solanum surattense*: a. Poricidal anthers, b. Pollen grain of long-styled flowers, c. Pollen grain of short-styled flowers, d. Ovules, e. & f. Buds infected with beetle, g. Beetles feeding on anthers, h. Dorsal view of beetle, i. Ventral view of beetle.

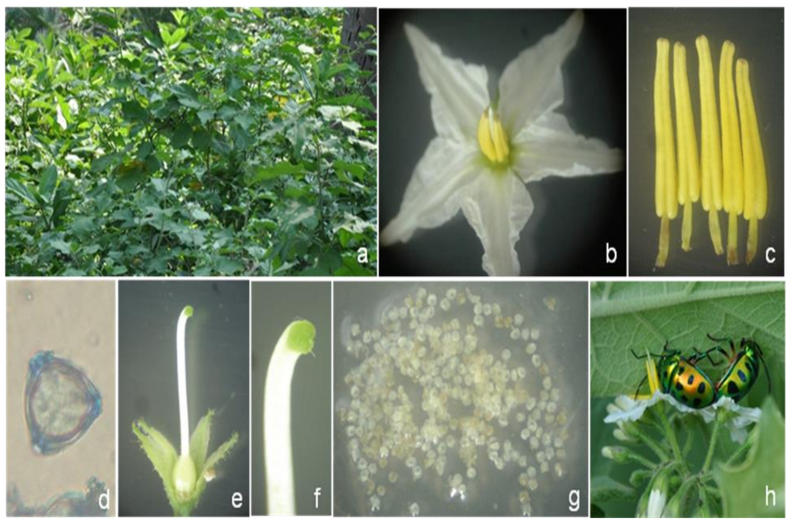

Figure 4 *Solanum torvum*: a. Habit, b. Long-styled flower, c. Stamens, d. Pollen grain, e. Pistil, f. Long style and stigma, g. Ovules, h. *Chrysocoris* sp. feeding on pollen/mating in the flowers.

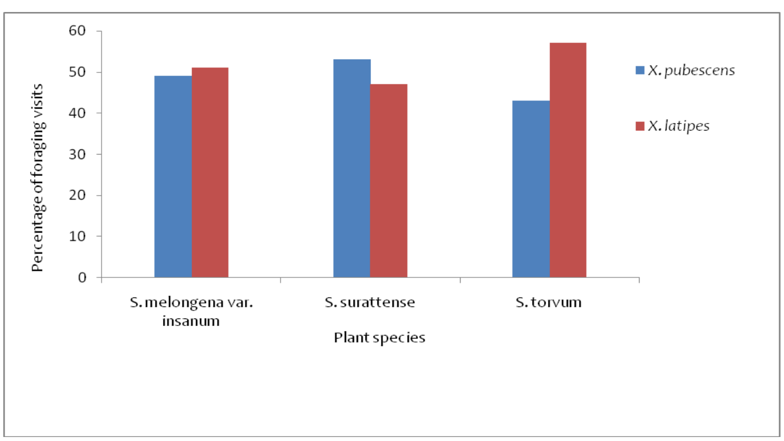

Figure 5 Daily percentage of foraging visits of *Xylocopa pubescens* and *Xylocopa latipes* on *Solanum melongena* var. *insanum, S. surattense* and *S. torvum*.

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Pollination

In all three *Solanum* species, the flower visitors included only carpenter bees, *Xylocopa latipes* and *X. pubescens* which visited the flowers from 0700 to 1700 h (Figure 1). The carpenter bees showed a gradual increase in foraging activity from morning towards noon and then a gradual decrease towards evening hours. These bees displayed buzzing behavior to gather pollen from the poricidal anthers. The buzzing length was very less at the fresh flowers and its length gradually increased towards evening hours. Accordingly, the pollen quantity in anthers gradually decreased from morning to evening. These bees upon landing on the anthers, grasped the latter with their hind legs, rotated on the flower to handle each anther separately to collect pollen. In this process, they performed vibrations with their wings by producing audible buzzes. Then, the pollen was released as puffs from the apical pores of the anthers and it is dispersed into the air surrounding the stigma in case of long-styled flowers. Sometimes, the pollen-laden ventral side of the bee body came into contact with the stigma resulting in pollination. Some pollen gradually descended through the tiny spaces between anthers causing incidental gravitation pollination in short-styled flowers. The flowers that were visited by these bees showed bruise marks on the anthers and these marks can be taken as indicators of bee visits that buzz the flowers. Large mass of pollen was visible on the hind legs of the bees visiting the flowers of all three plant species. Occasionally, *Amegilla* bees also visited the flowers for pollen collection; they did buzz the flowers while collecting pollen which is released from the apical pores of the anthers. They also effected pollination and hence they are treated as supplementary pollinators.

A beetle (unidentified) used *S. surattense* buds as its breeding site and it gathered milky pollen from the un-dehisced anthers by initially making puncturing and then making holes into the anthers (Figure 3e-i). The beetle is exposed upon anthesis and it still continued its pollen feeding activity. Bud infestation rate by this beetle is 30%. The infested flowers did not set fruit and hence the beetle is considered to be negatively affecting the success of sexual reproduction. A hemipteran polyphagous jewl bug, *Chrysocoris* sp. (Scutelleridae) uses the flowers of *S. torvum* as feeding and mating site (Figure 4h). Its flower feeding activity involves the consumption of pollen and delicate petals. The flowers were damaged by this bug are not involved in fruit set and hence this bug also affects the success rate of fruit set through sexual reproduction in *S. torvum*.

3. DISCUSSION

In *Solanum* genus, most species display a typical floral morphology involving the production of yellow poricidal anthers with rigid walls contrasting with the corolla color. The flowers of this genus are excellent models for buzz-pollination effected mostly by carpenter bees (Harder and Barclay 1994). In the present study also, the stamens are yellow with rigid walled poricidal anthers in all three *Solanum* species but the corolla color is bluish-violet in *S. melongena* var. *insanum*, purple in *S. surattense* and white in *S. torvum*. The contrasting color appears to be advantageous for these species to attract the appropriate pollinating bees. All the three plant species offer only pollen as a floral reward due to non-production of nectar. The pollinating bees could get only pollen from the flowers and hence the pollinating bees use these species as exclusive pollen source, especially for making bee bread by female bees for raising their brood. Further, the pollinating bees in all three *Solanum* species are carpenter bees of the genus *Xylocopa*. These bees are consistent and efficient in pollen collection by vibrating the anthers from below to push out the pollen from apical pores. In this process they make audible buzzes which vary in length according to the time of the day which in turn is related to the availability of pollen quantity in the flowers, the duration of audible buzz is more on fresh or newly open flowers due to availability of full load of pollen in the anthers. The study indicates that all three Solanum species are adapted for pollination by carpenter bees. However, other bees may also use them as pollen source according to the availability of floral resources in the habitat. In this context, it is to be noted that *Amegilla* bees occasionally use these plant species as pollen source and also act as efficient pollinators on par with *Xylocopa* bees and hence, they can be treated as additional pollinators.

Dupont and Oleson (2006) reported that *Solanum vespertilio* and *S. lidii* produce dimorphic flowers with long-styled and short-styled ones on the same plants. The long-styled flowers are functionally hermaphroditic while the short-styled flowers are functionally male and hence fruit set occurs only in long-styled flowers. In this study also, all three *Solanum* species exhibit similar functional state of flowers indicating that these species are andromonoecious. Fruit set in long-styled flowers is more in open-pollination which is effected by pollinating bees indicating that there is a possibility for self-compatibility that facilities the promotion of fruit set rate. Dulberger et al., (1981) reported that *S. marginatum* is andromonoecious characterized by long-styled hermaphrodite flowers and female-sterile medium- or short-styled flowers and this sexual system does not promote cross-pollination. These authors also stated that in female sterile flower type, the development of most ovules is arrested at megasporocyte stage itself and hence this flower type increases pollen/ovule ratio and aids in attracting and sustaining pollinator bees to ensure high fertilization rate of flowers. Similar situation appears to be in existence in all the three *Solanum* species studied. The female sterile short-style flowers in these species make available more pollen for transport through polling bees and also to

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compensate the pollen loss due to pollen collection by bees and during pollen release into the air while the buzzing activity displayed by bees. Further, in case of *S. surattense* and *S. torvum*, the beetle/jewel bug pollen feeding activities reduce the availability of pollen for pollen collection by pollinating bees and also for pollination purpose. Therefore, all three *Solanum* species are andromonoecious, self-compatible and pollinated by carpenter bees.

4. CONCLUSION

All three *Solanum* species are andromonoecious, self-compatible in hermaphrodite flowers and pollinated by carpenter bees. Andromonoecy is not perfectly evolved as female sterile flowers are produced in a small percentage at plant level. However, female sterile flowers as pollen donors provide abundant availability of pollen for self- and/or cross-pollination in hermaphrodite flowers. Carpenter bees are quite appropriate for pollination in these species since they exhibit buzzing behavior by vibratile movement of their wings to release pollen from apical pores of the anthers. Any other bees visiting the flowers act as additional pollinators only. Since the flowers of all three Solanum species do not produce nectar, they serve as exclusive pollen source for carpenter bees or any other bees that visit the flowers of these species.

Author's contributions

Both authors contributed equally.

Ethical approval

Solanum melongena var. *insanum, S. surattense* and *S. torvum* plants were used in this research. These plants gathered from Araku area in the State of Andhra Pradesh, India. Ethical Guidelines for plants & plant materials are followed in the study.

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Conflicts of interests

The authors declare that there are no conflicts of interest.

Data and materials availability

All data associated with this study are present in the paper.

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